

RESPONSE OF GRASSLAND VEGETATION ON SANTA CRUZ ISLAND TO REMOVAL OF FERAL SHEEP

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ABSTRACT

We measured biomass and frequency of herbaceous species before and 12 years after removal of feral sheep from a grassland on Santa Cruz Island, California. Native grasses, especially *Stipa* spp., increased dramatically following sheep removal whereas all exotic grasses except *Avena* spp. decreased, probably reflecting the competitive ability of native grasses as well as differential vulnerability to grazing. Native forbs showed a mixed response, with some species increasing but many decreasing, perhaps because some native forbs benefit from grazing. Almost all exotic forbs decreased, likely because these species benefit from herbivores and their activities. Our results provide encouraging evidence that an island grassland dominated by exotic species has the potential for recovery from severe overgrazing.

Key Words: Annual grass, exotic species, feral sheep, grassland, grazing, herbivory, island restoration, *Stipa*.

Feral herbivores, especially goats and sheep, have been introduced to numerous islands around the world, and resulting overgrazing has caused major impacts on island vegetation (Coblentz 1978; Scowcroft and Giffin 1983; Wardle et al. 2001). Because of these impacts, feral herbivores have been eradicated from many islands (Bullock et al. 2002; Campbell and Donlan 2005; Carrion et al. 2006), which has often resulted in a dramatic recovery of native vegetation. Most studies of vegetation recovery have focused on shrub or woodland communities (e.g., Wehtje 1994; Bullock et al. 2002; Reddy et al. 2012). The relatively few studies that quantified plant recovery in grasslands found a general pattern of increased cover or frequency of native vegetation, often dramatically so, following the removal or exclusion of feral goats or sheep (Baker and Reeser 1972; Meurk 1982; Klinger et al. 2002). However, several researchers have expressed concern about the proliferation of exotic herbaceous species following release from grazing pressure and how that proliferation might hinder the recovery of native species (Scowcroft and Hobdy 1987; Kessler 2002; Klinger et al. 2002; Knapp et al. 2009).

Santa Cruz Island, the largest (249 km²) of the eight Channel Islands located offshore of southern California, supported a large population of domestic sheep (*Ovis aries*). Sheep were introduced in the 1850's, reached numbers of 50,000 or more by the late 1800's, and became feral by the 1920's (Van Vuren and Bakker 2009). Sheep

grazing had a major effect on island vegetation; for example, one grassland had 40% of the soil surface denuded and had an altered community composition on the 60% that supported vegetation (Van Vuren and Coblentz 1987). All sheep were removed, first on the western 90% of the island during 1981–1989, and then on the eastern 10% of the island during 1997–2001, with a total of 47,000 sheep removed (Schuyler 1993; Faulkner and Kessler 2011). Recovery of woody vegetation has been dramatic (Wehtje 1994; Cohen et al. 2009), but response of grassland species has received limited study (Klinger et al. 2002). On Santa Cruz Island, as on mainland California, grasslands once dominated by native perennial grasses have become dominated by exotic annual grasses (Junak et al. 1995), leading to the hypothesis that exotic grasses are competitively superior (Seabloom et al. 2003; Corbin and D'Antonio 2004). Evaluation of the initial response (≤ 5 years) by grasslands on Santa Cruz Island to sheep removal suggested an increase in annual grasses at the expense of native species (Klinger et al. 2002). Consequently, the potential for dominance of exotic species after removal of feral sheep from Santa Cruz Island may be of particular importance. Our objective was to evaluate grassland vegetation before and 12 years after removal of feral sheep, in order to assess the potential for recovery of a community dominated by exotic species.

METHODS

Santa Cruz Island is characterized by rugged topography and an east-west system of interior

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valleys, dominated by the large Central Valley, which are bordered by the Northern Ridge (elevation 750 m) and Southern Ridge (elevation 465 m). Climate is an oceanic, Mediterranean type characterized by hot, dry summers and cool, wet winters. Most of the 51-cm average annual precipitation falls from November through April (Boyle and Laughrin 2000). The island is botanically diverse, with 627 species of vascular plants of which 157 are exotic (Junak et al. 1995). Several plant communities have been described (Junak et al. 1995), with grassland (46%) and chaparral (31%) being the most common in 1980 in terms of proportion of the island covered (Minnich 1980). Our study was conducted in Ram Canyon, a 2-km long drainage that begins at the crest of the Northern Ridge and drains southward to the Central Valley. Our study area was at an elevation of 300–350 m near the headwaters of the canyon (34°01'30"N, 119°45'45"W), where tributaries join from the west, northwest, and northeast. Vegetation in the study area was classified in 1980 as mostly grassland with scattered patches of chaparral dominated by *Quercus pacifica* Nixon & C. H. Mull and *Ceanothus megacarpus* Nutt. var. *insularis* (Eastw.) P. H. Raven (Minnich 1980). Density of feral sheep in this area was estimated at about 2/ha, which is considered exceptionally high (Van Vuren and Coblenz 1989; Schuyler 1993). Feral pigs (*Sus scrofa*) were present on Santa Cruz Island throughout our study, but they were uncommon in our study area and we found no evidence of pig rooting in or near any of our quadrats.

We sampled vegetation 2–13 April 1980, during the peak of the growing season, in order to determine forage availability in a study of feral sheep diets (Van Vuren and Coblenz 1987). We used a stratified-random design in our sampling. We chose nine grassland sites that appeared representative of the vegetation in the area; these sites were distributed throughout an 8-ha area on the middle and lower slopes of the canyon, hence slope exposure varied among sites. Within each site we randomly located 0.75×1.50 m quadrats, six at each of the first eight sites and two at the ninth site, for a total of 50 quadrats. We identified all green herbaceous species in each quadrat to the lowest taxon feasible, clipped them at ground level, and weighed them to the nearest gram; nomenclature followed Baldwin et al. (2012). A sample of each plant species was clipped, weighed, dried at 65°C for 24 hours, and then reweighed to obtain dry biomass. Feral sheep were removed from the area during July–December 1984 (P. T. Schuyler, personal communication), and fencing prevented recolonization by sheep remaining on other parts of the island (Schuyler 1993). We returned to our study area during 4–13 April 1996 and sampled all nine

sites again using the same procedures, including randomizing the location of quadrats within each site. Winter rainfall on Santa Cruz Island differed between 1980 and 1996 (Boyle and Laughrin 2000). Precipitation during November through March totaled 64.1 cm for 1980 (13.3 cm of this falling in March), compared with 35.7 cm (4.7 cm in March) for 1996.

We calculated mean biomass (g/m^2 , dry basis) by averaging among all 50 quadrats for each species, and we calculated frequency of occurrence among all 50 quadrats for each species. We grouped species according to whether they were native or exotic (Junak et al. 1995). For most species this was straightforward, but some taxa identified only to genus contained both native and exotic species. Two species of *Festuca* were exotic and common, and two were native and scarce (Junak et al. 1995); hence, we classified *Festuca* spp. as exotic. Of the nine species of *Bromus*, three of five exotic species were common, but only one of four native species was common; the remaining five species were rare, whether native or exotic. Hence, we classed *Bromus* spp. as exotic, though we recognize that *B. carinatus* Hook. & Arn. var. *carinatus*, the common native species, could have been in our quadrats but not identified. We combined *Pseudognathium* spp. and *Gamochaeta* spp. into one group considered to be native, because several of the seven native species in the two genera were common, whereas the one exotic species was considered occasional and generally occurred in sites more mesic than ours (Junak et al. 1995). We compared mean biomass between 1980 and 1996 for plant groups (native grasses, exotic grasses, native forbs, exotic forbs) using a t-test. Statistical comparisons for individual species were either precluded or rendered of questionable value by the large number of zeros in the data.

RESULTS

Total biomass increased substantially after removal of feral sheep, from 29.8 g/m^2 in 1980 to 51.9 g/m^2 in 1996. However, native species differed from exotic species in their responses to sheep removal. Biomass of exotic grasses increased by only 32%, from 20.3 g/m^2 to 26.8 g/m^2 , a difference that fell short of statistical significance ($t = 1.76$, $P = 0.082$). In contrast, native grasses increased from 0.2 g/m^2 to 18.1 g/m^2 , an increase of nearly two orders of magnitude that was significant ($t = 2.80$, $P = 0.007$). Native forbs increased 59%, from 3.7 g/m^2 to 5.9 g/m^2 , though the difference was not significant ($t = 1.21$, $P = 0.110$). Exotic forbs decreased 80%, from 5.6 g/m^2 to 1.1 g/m^2 , a difference that was significant ($t = 3.28$, $P < 0.001$).

Individual taxa varied considerably in their response to removal of feral sheep. The proliferation

TABLE 1. DRY BIOMASS AND FREQUENCY OF PLANTS AMONG 50 QUADRATS IN A GRASSLAND ON SANTA CRUZ ISLAND, CALIFORNIA DURING APRIL 1980 AND APRIL 1996.

Taxa	1980		1996	
	g/m ²	Frequency	g/m ²	Frequency
Native grasses				
<i>Aristida</i> spp.	0.0	0.00	2.0	0.10
<i>Stipa</i> spp.	0.2	0.12	16.1	0.32
Exotic grasses				
<i>Avena</i> spp.	1.0	0.60	18.7	0.94
<i>Bromus</i> spp.	11.4	1.00	6.9	0.72
<i>Festuca</i> spp.	5.4	0.86	1.0	0.32
<i>Hordeum murinum</i> L.	1.1	0.36	0.0	0.00
<i>Lamarckia aurea</i> Moench	1.4	0.82	0.2	0.24
Native forbs				
<i>Acmispon strigosus</i> (Nutt.) Brouillet	0.1	0.22	0.0	0.00
<i>Acmispon wrangelianus</i> (Fisch. & C.A. Mey.) D.D. Sukoloff	0.1	0.08	2.7	0.32
<i>Acourtia microcephala</i> DC.	0.7	0.02	0.0	0.00
<i>Apiastrum angustifolium</i> Nutt.	0.0	0.00	<0.1	0.02
<i>Astragalus didymocarpus</i> Hook. & Arn.	0.2	0.40	0.3	0.36
<i>Claytonia perfoliata</i> Willd. subsp. <i>perfoliata</i>	0.1	0.10	<0.1	0.02
<i>Croton setigerus</i> Hook.	0.3	0.58	1.0	0.14
<i>Daucus pusillus</i> Michx.	0.3	0.52	0.0	0.00
<i>Dichelostemma capitatum</i> (Benth.) Alph. Wood subsp. <i>capitatum</i>	<0.1	0.10	<0.1	0.12
<i>Eucrypta chrysanthemifolia</i> (Benth.) Greene var. <i>chrysanthemifolia</i>	0.2	0.40	0.0	0.00
<i>Galium</i> spp.	<0.1	0.04	0.0	0.00
<i>Gilia</i> spp.	0.0	0.00	<0.1	0.02
<i>Lasthenia californica</i> Lindl.	0.1	0.24	0.0	0.00
<i>Layia platyglossa</i> (Fisch. & C.A. Mey.) A. Gray	<0.1	0.16	<0.1	0.02
<i>Logfia filaginoides</i> (Hook. & Arn.) Morefield	0.9	0.66	0.7	0.18
<i>Lupinus bicolor</i> Lindl.	<0.1	0.06	0.6	0.40
<i>Marah</i> spp.	<0.1	0.02	0.0	0.00
<i>Phacelia</i> spp.	0.0	0.00	<0.1	0.02
<i>Pseudognaphalium</i> spp., <i>Gamochaeta</i> spp.	0.2	0.42	0.1	0.16
<i>Pterostegia drymarioides</i> Fisch. & C.A. Mey.	<0.1	0.02	<0.1	0.02
<i>Thysanocarpus curvipes</i> Hook.	0.0	0.00	0.1	0.14
<i>Trifolium</i> spp.	0.5	0.70	0.3	0.26
Exotic forbs				
<i>Capsella bursa-pastoris</i> L.	<0.1	0.04	0.0	0.00
<i>Cerastium glomeratum</i> Thuill.	0.2	0.16	0.0	0.00
<i>Erodium</i> spp.	1.4	0.90	0.2	0.36
<i>Hypochaeris glabra</i> L.	3.0	0.86	0.0	0.00
<i>Medicago polymorpha</i> L.	0.2	0.24	0.0	0.00
<i>Silene gallica</i> L.	0.6	0.60	0.0	0.00
<i>Sonchus asper</i> (L.) Hill subsp. <i>asper</i>	0.0	0.00	0.9	0.40
<i>Stellaria media</i> (L.) Vill.	0.1	0.12	<0.1	0.08

of native grasses resulted from a dramatic increase in both biomass and frequency of *Stipa* spp., as well as the appearance of *Aristida* spp. (Table 1). For exotic grasses, *Avena* spp. increased in both biomass and frequency, while the remaining species either decreased in both measures (*Bromus* spp., *Lamarckia aurea* Moench, and *Festuca* spp.) or were not detected at all (*Hordeum murinum* L.; Table 1).

Several native forbs showed a low frequency of occurrence among quadrats in both 1980 and 1996 (e.g., *Acourtia microcephala* DC., *Apiastrum angustifolium* Nutt., *Galium* spp., *Gilia* spp., *Marah* spp., *Phacelia* spp., and *Pterostegia drymarioides* Fisch. & C. A. Mey.), hence either

these species did not respond to sheep removal or were at such a low frequency that our sampling protocol did not detect a response (Table 1). Two species (*Acmispon wrangelianus* (Fisch. and C.A. Mey.) D.D. Sokoloff and *Lupinus bicolor* Lindl.) showed substantial increases in both biomass and frequency. Many native forbs, however, decreased in biomass, frequency, or both between 1980 and 1996, including several native forbs that were common (frequency ≥ 0.40) in 1980 (e.g., *Daucus pusillus* Michx., *Eucrypta chrysanthemifolia* (Benth.) Greene var. *chrysanthemifolia*, *Logfia filaginoides* (Hook. & Arn.) Morefield, *Pseudognaphalium* spp., *Gamochaeta* spp., and *Trifolium* spp.). *Croton setigerus* Hook., one of

the most common native forbs in 1980, decreased in frequency by 1996 but increased in biomass. One common native forb, *Astragalus didymocarpus* Hook. & Arn., remained relative unchanged in biomass and frequency between 1980 and 1996 (Table 1).

All but one exotic forb decreased in both biomass and frequency between 1980 and 1996 (Table 1); three taxa in particular, *Erodium* spp., *Hypochaeris glabra* L., and *Silene gallica* L., were among the most important forbs, native or exotic, in 1980 in terms of both biomass and frequency but were greatly reduced or absent in 1996. One exotic forb, *Sonchus asper* (L.) Hill subsp. *asper*, was not identified in 1980 but was common in 1996 (Table 1).

DISCUSSION

The increase in biomass of grassland vegetation shown in 1996, 12 years after removal of feral sheep, is not surprising given the high density of sheep present in 1980; the area was considered to be severely degraded due to long-term overgrazing (Van Vuren and Coblenz 1987). Indeed, the response might have been greater if not for relatively dry conditions during 1996. Rainfall in 1996 was 38% below the long-term average, whereas rainfall in 1980 was 26% above the average (Boyle and Laughrin 2000). On Santa Cruz Island, cover of herbaceous vegetation is positively correlated with annual rainfall (Klinger et al. 2002).

As a group, exotic grasses showed only a modest increase in biomass, and that increase was attributable entirely to one genus, *Avena*, which is represented by two annual species (*A. barbata* Link and *A. fatua* L.) that are common on the island (Junak et al. 1995). *Avena* is especially vulnerable to heavy grazing pressure (Heady 1988), which characterized conditions in 1980, and it also may be a good competitor after release from grazing because of its tall stature (Menke 1992). All other exotic grasses declined in both biomass and frequency; some of these grasses might be poor competitors in the absence of sheep disturbance, which is the case for *Lamarckia aurea* (Crampton 1974).

In contrast to exotic grasses, native grasses showed a dramatic increase in both biomass and frequency, especially *Stipa*, which is represented by three perennial species (*S. cernua* (Stebbins & Love) Barkworth, *S. lepida* Hitchc., and *S. pulchra* Hitchc.) (Junak et al. 1995). This result is somewhat surprising, since the wholesale replacement of native perennial grasses by exotic annual grasses and forbs throughout much of California during the 19th century has been hypothesized to have resulted because native grasses are inferior competitors (Seabloom et al. 2003; Corbin and D'Antonio 2004). However, *Stipa pulchra* is a

good colonizer of bare soil (Bartolome and Gemmill 1981; Seabloom et al. 2003), which was common in our study area in 1980 due to grazing and trampling by feral sheep (Van Vuren and Coblenz 1987). Once established, native perennial grasses can be strongly competitive with exotic annual grasses (Seabloom et al. 2003; Corbin and D'Antonio 2004), especially at coastal sites where the summer drought typical of California's Mediterranean climate is moderated by marine influences (Corbin and D'Antonio 2004). Our study site was located only 3.3 km from the coast.

Native forbs varied greatly in their response to removal of feral sheep. Much of this variation likely resulted from differential rainfall between years and its effect on germination and growth of annual species. Most of the native forbs in our study are annuals, as are all of the exotic forbs (Junak et al. 1995). In annual grasslands on the mainland, species composition can vary greatly from year to year, especially in response to rainfall (Talbot et al. 1939; Pitt and Heady 1978; Heady 1988). However, some of the variation in native forb response likely resulted from the cessation of grazing. Most native forbs may not have been greatly impacted by sheep herbivory, since native forbs other than *Croton setigerus* were rarely eaten by feral sheep (Van Vuren and Coblenz 1987). Consequently, many native forbs may have benefited from grazing that reduced mulch and suppressed competitors (Coleman and Levine 2007), potentially explaining the decline in several species after sheep were removed. Research on grasslands elsewhere in California showed that grazed sites have a higher richness and abundance of native forbs (Hayes and Holl 2003).

Two native forbs, however, increased in both biomass and frequency. *Acmispon wrangelianus* may have benefited from removal of feral sheep; in a mainland California grassland, this species increased in abundance when herbivores were excluded (Hobbs et al. 2007). The response of *Lupinus bicolor* is somewhat surprising, since Thomsen et al. (1993) found that grazing had a positive rather than a negative effect on density. *Croton setigerus* increased in biomass but decreased in frequency, perhaps because it was a highly preferred food of feral sheep (Van Vuren and Coblenz 1987) but is also associated with disturbed areas (Junak et al. 1995). Hence, a lack of herbivory coupled with a lack of disturbance in 1996 may have resulted in fewer but larger plants.

Exotic forbs as a group showed a dramatic decrease following sheep removal, a finding consistent with that of Klinger et al. (2002) for other grasslands on Santa Cruz Island. Research in mainland California indicates that several of these species likely benefit from the presence of

herbivores and their activities, especially soil disturbance and the removal of mulch. *Erodium* spp. decreased markedly in cover when herbivores were excluded (Talbot et al. 1939); *Medicago polymorpha* L. was more frequent on disturbed sites than on relatively undisturbed sites (Schiffman 1994); and the presence of mulch depressed seed production in *Erodium* spp. (Rice 1985) and interfered with seed germination in *Hypochaeris glabra* (Heady 1956) and *Capsella bursa-pastoris* L. (Bergelson 1990). Similarly, Harrison et al. (2003) found that grazing enhanced the richness of exotic forbs. The increase in *Sonchus asper* subsp. *asper* was unexpected, since the species disappeared from a grassland in Britain 13 years after herbivores were excluded (Watt 1981) and the congeneric *S. oleraceus* L. declined on nearby San Miguel Island between 6 and 25 years after feral livestock were removed (Corry and McEachern 2009). Perhaps *Sonchus asper* subsp. *asper* will decline as well in our study area, given enough time.

Our study suffered from several limitations. The composition of California annual grasslands can vary greatly between years and also seasonally, whether grazed or not (Talbot et al. 1939; Heady 1988), hence our measures may not have been representative. Further, our results reflect only two points in time, providing a limited ability to ascertain the patterns of change during intervening years, especially if those patterns are not linear. Finally, we sampled only one location, which may not be representative of other grasslands on Santa Cruz Island because of variation in topography and grazing history (Klinger et al. 2002). Klinger et al. (2002) sampled several grasslands on Santa Cruz Island 1–5 years after sheep removal and found that exotic species, especially grasses, had increased in frequency, were dominant, and potentially were displacing native species. Our results, showing a proliferation of native grasses and a decline in most exotic species, may reflect geographic variation in grassland response, or it may reflect an additional 7–11 years of time. Time frames longer than 5 or even 12 years may be necessary to understand grassland recovery from overgrazing (Hobbs et al. 2007). Despite these limitations, our results provide encouraging evidence indicating that 12 years after removal of feral sheep from an island grassland, most exotic species had decreased and some native species, especially native grasses, had increased.

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